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The pollination of the palm *Archontophoenix Cunninghamii*

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Bordering the path which led up from the tramline to the front steps of the house in which I lived near Almirante, in the province of Bocas del Toro in western Panama, stood six stately palm trees of the species *Archontophoenix Cunninghamii*, Wendl and Drude. Unfortunately for the effect they produced, all were not of the same age. The largest was a magnificent specimen which measured 64 feet to the top of the leafy crown, and was 11 inches in circumference at breast height. The straight, clean, columnar trunk was prominently ringed by the crowded scars of the fallen leaves, and the closely encrusting lichens which covered much of its surface gave it a light gray color. At the upper extremity of the trunk three or four richly branched spadices stood out almost horizontally, with the slender, flexuous branches pendent beneath the thicker main axis. Above the spadices the trunk appeared to be continued by a smooth, green extension, about six feet long, thicker than the older portion below. This apparent prolongation of the trunk was in reality a false-stem made up of the tubular, concentric sheaths of the leaves. From the apices of their sheaths sprang the gracefully plumed fronds, which measured about 11 feet long by 6 feet broad (Plate I).

Many palms, including *Archontophoenix*, the royal palm, and the stilt-palm *Attalea*, resemble the banana in the possession of a prominent false-stem, but there are a number of important differences between the two types of plants. While the false-stem of the banana at any age springs from near or below the surface of the ground, at the apex of a bulbously swollen rhizome, that of the palm is raised on its woody caudex, in old plants, many feet above the ground. In the former the leaf-sheaths which form this false-stem are open, crescentic in cross-section and closely overlapping, in the latter they are closed,

tubular and concentric. In both cases the new leaves are formed at the center of this false-stem, completely hidden from view, and only push out from the top when they are practically mature. In respect to the position of their inflorescences, the two types of plants differ fundamentally. The single inflorescence which culminates the growth of each banana "tree" is formed in the center of the false-stem and, after performing a long upward journey, emerges at the top, while in *Archontophoenix*, once the tree has reached reproductive maturity, an inflorescence is generally formed in the axil of each leaf, and they are exposed successively as the leaf-sheaths split open and fall away.

While the youngest leaf stands almost erect, the older ones gradually droop, and finally the oldest, hanging vertically downward, begins to die and turn brown. The increasing pressure of the young leaves and inflorescences, continually being formed within, finally causes the thick, leathery sheath, over 4 feet long, to split from top to bottom down the side opposite to the attachment of the lamina. Meanwhile the base of the sheath is becoming detached from the stem so as to leave a circular scar. As the dying leaf falls away the elongated spathes which enclose the inflorescence are revealed standing upright in the axil of the sheath. The first spathe may split down either the inner or outer side, and falls away, according to my observations in Panama, from 8 to 16 days after the frond has dropped. The spadix is still enclosed in a second, similar spathe, which generally bursts and falls a day or two after the first. These spathes are green, thick and leathery, and completely closed, and the inflorescence is so crowded within that there is not the slightest waste space. The flower buds are sharply angular as a result of the pressure to which they have been subjected during their development (Fig. 1). The spathes are burst simply by the swelling of the spadix within them, and there is no preformed line of dehiscence.

Only one of the five fruiting palms was low enough for me to reach the inflorescences when standing on top of an eighteen foot stepladder, and this tree was kept under observation from January until June, 1929. Once they had escaped from their spathes, the numerous, slender, whip-like branches of the inflorescence hung beneath the short, thick, horizontal main axis.

Archontophoenix Cunninghamii, from a cultivated tree growing near Almirante, Panama. January 31, 1929.

Along the length of these woody, flexuous branches the flowers were arranged in groups of three. These clusters were arranged spirally; the divergence was probably either 2/5 or 3/8 of the circle, but because of the flexuosity of the axis it was not possible to determine with certainty which was the actual value.

Fig. 1. The spathe and spadix of *Archontophoenix*. At left the inner spathe after removal from the outer. In center, the spathe splitting and exposing the spadix, several branches of which have escaped. At right, the spadix after removal from the spathe, showing the tight packing of the flower buds. x about 1/9.

The triad of flowers, representing a principal and two lateral accessory buds, stood in the axil of a small and inconspicuous white bract. Each group consisted of a central pistillate flower with a staminate flower on either side of it. Occasionally there

occurred clusters of four, with two staminate flowers on one side or the other. The staminate flowers were invariably the first to open. Starting at the base of the pendent branch, and following the spiral which includes the flower groups downward to the apex, I found that in each triad the staminate flower

Fig. 2. The flowers of *Archontophoenix*. At left, a portion of a branch of the inflorescence showing the first staminate flower of several triads fully open. The second staminate flower and the pistillate flower in each of these triads are still in the bud, while in some triads no flower has yet expanded February 13, 1929. At right, a portion of a branch of the same inflorescence after all staminate flowers have fallen, showing the pistillate flowers with receptive stigmas February 28. Slightly enlarged.

which was first encountered on this descending course was always the first to expand. The staminate flower on the side from which the spiral leaves the group never opened until the other

had fallen, and the pistillate not until both had dropped, and so in each group, there was never more than a single open flower at any one time. The staminate flower consisted of from 12 to 16 stamens arising from a mound of tissue at its center, surrounded by three rather conspicuous woody, white, deltoid petals 5 mm. long, beneath which were hidden three additional scale-like perianth segments.

The first staminate flowers were generally found to be open as soon as the inflorescence had escaped from the enclosing spathes. Thereafter a new set opened every morning, following the sequence set forth above, and by evening there was a rain of spent flowers with withered anthers beneath each flowering tree. The opening of new staminate flowers continued for from 12 to 14 days after the escape of the inflorescence, when the buds of this kind were practically exhausted, and the pistillate flowers now began to function. These did not become receptive until most of the staminate flowers of the inflorescence had fallen. Perhaps it is not quite accurate to speak of the "opening" of the pistillate flowers, (unless one means their stigmas), for the six white, scale-like divisions of the perianth did not actually expand, but the ovoid ovary closely embraced by them swelled until it spread them apart a bit, and the three sessile stigmas peeped forth from between them. They were stigmatic along their inner faces, and a drop of fluid collected in the angle between them. The inflorescence bore receptive pistillate flowers for a period of 5 or 6 days after the majority of the staminate had fallen. Thus the period of anthesis of the inflorescence considered as a whole was 18 or 19 days, and the time during which it bore functional staminate flowers about double that for the pistillate flowers.

The course of events which has just been described was rendered somewhat irregular by the behavior of those flowers at the extremities, especially at the apex, of each branch of the inflorescence. After all of the staminate flowers had fallen from the main portion of the branch, and the pistillate flowers had begun to become receptive, there were generally a few lingering staminate flowers at these extremities. Different branches did not always enter the pistillate stage on the same day, so there was a certain amount of overlapping between the staminate stage of one branch and the pistillate stage of its neighbors.

Nevertheless, each spadix was for a period of two weeks, or a little less, exclusively staminate, then followed a few days when it was preponderately pistillate, but bore a few belated male flowers, and finally, after these had fallen, it became exclusively pistillate. Since each tree bore only a single flowering spadix at the time, cross pollination between neighboring trees must have been the rule. The different trees were generally in different phases of flowering, so those inflorescences which had most recently escaped could furnish pollen to the pistillate flowers of spadices on other trees which had burst their spathes a week or two earlier.

The following table will serve to recapitulate the behavior of this tree:

January 31, 1929. Leaf fell exposing inflorescence enclosed in its spathes.

February 8. Outer spathe fell.
10. Inner spathe fell, staminate flowers open and visited by bees.
22. Staminate flowers mostly fallen, the first pistillate flowers receptive.
25. Staminate flowers all spent.
28. Pistillate flowers practically all expanded.

March 21. Second leaf fell exposing inflorescence (Details of the anthesis of this spadix were not followed).

April 16. The fruits of the inflorescence which came into bloom about January 1 are now ripe (after 3 1/2 months).
24. Third leaf fell exposing inflorescence.

May 2. Outer spathe burst.
3. Both spathes fell and the first staminate flowers opened.
17. A few pistillate flowers, on branches from which all staminate flowers had fallen, were receptive.
19. All but a few straggling staminate flowers have fallen.
22. Pistillate flowers practically all expanded.
31. Fourth leaf fell exposing inflorescence.

June 6. I left Almirante and discontinued observations.

Whatever may be the principal agent of pollination in the palm's native habitat in Queensland and New South Wales, at Almirante the little black, stingless bee, *Trigona amalthea* (Olivier) plays the chief rôle. Other visitants to the flowers are flies, mosquitoes and small wasps, but the bees far outnumber all of the others together, and by their systematic harvest of both pollen and nectar are apparently the only ones fitted to play an important part in cross-pollination. This bee (and related species) is so important as a pollinating agent of many plants in Central America, and so interesting in its habits, that it deserves a few words devoted to itself. A colony of them inhabited an enormous "nigger-head" termites' nest, the work of a species of *Nasutitermes* (voluntarily or involuntarily abandoned by the latter), situated in a large cacao tree not more than fifty yards from the nearest palm. It was one of the largest nests of this type I remember having seen, ellipsoidal in shape, and measured 3.5 feet in height by half as thick. The bees had provided an entrance on one side in the form of a large, funnel-shaped aperture. Although stingless and apparently harmless, even when disturbed, away from their hive, when their home is molested they sally forth in numbers and, attaching themselves to the hair or skin or clothing of the intruder, attempt a bite which is more annoying than painful, at the same time advertising their anger by a persistent, high-pitched buzz. Desiring to clear some branches from the vicinity of this nest, for the purpose of a photograph, I was advised to do the work at night, but even then was not immune from an angry sortie by its inhabitants.

The staminate flowers in mass have a faint but agreeable fragrance which is difficult to describe. Perhaps attracted by this, the bees swarm over them in large numbers, collecting the pollen into great swollen masses on their hind legs. The pollen grains possess a perfectly smooth exine and are dry and dusty rather than cohesive. They do not appear particularly well adapted for either insect or wind pollination. When examined dry, each has the form of a grain of wheat, a resemblance which is further heightened by a deep furrow down the inner face. Placed in water the grain swells out and the furrow is represented by a very faint line. Bees bearing enormous loads of this pollen, which they secure from neighboring trees, in their pollen bas-